The Evolution and Classification of Roses

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The paper on *Rosa* by Dr. C. C. Hurst of England, presented to the Genetics Congress in Berlin in 1927[1], is of extraordinary interest to botanists. It offers a classification of the genus *Rosa*, based mainly on cytological evidence, or at least the concurrance of external characters with cytological conditions. Starting with the admitted fact that the gametes of roses carry a minimum of seven chromosomes, it is shown that when this number is exceeded we have multiples of seven, even up to fifty six. The forms with the minimum number, fourteen in the somatic cells, are called diploids; those with higher numbers polyploids, or more specifically triploids, tetraploids, pentaploids, etc. This of course, parallels what has been found in other organisms. In all 1,006 different species and forms of *Rosa* have been examined cytologically, or had been when Hurst's paper was written. Of these Hurst himself examined 674, and the whole series represents all the recognized sections and subsections of the genus. Beginning with the diploids, it is observed that they fall into nine distinct groups. Four of these are so distinct that they are excluded from *Rosa* altogether, under the following generic names:

Hulthemia, for *H. persica* (Michx.) of the deserts of Central Asia.

Platyrhodon, for *P. microphylla* (Roxb.) of China and Japan.

Ernestella, for *E. bracteata* (Wendl.) of China and *E. involucrata* (Roxb.) of India and Burma, the latter regarded as a subspecies.

Hesperhodos, for *H. minutifolia* (Engelm.), *H. stellata* (Wooton), and *H. stellata mirifica* (Greene) all of the arid region of North America. Hurst treats Wooton's *R. stellata* and Greene's *R. mirifica* as subspecies of *H. minutifolia.*

There now remain five groups, true members of *Rosa,* which are designated AA, BB, CC, DD, EE, with gametes A, B, C, D, E. The characters of all of these groups are cited; most are morphological, but some physiological, as the late ripening of the fruits.

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[1] C. C. Hurst. Differential Polyploidy in the Genus Rosa, L. Verh. Internat. Kongresses f. Vererbungslehre, Berlin, 1927. Supplbd. Zeits. f. induktive Abstammungs und Vererebungslehre. 1928. pp. 866-906.

The AA forms are numerous, including *R. sempervirens* L. of S. Europe and N. Africa, *R. arvensis* Huds. of Europe, *R. multiflora* Thunb. of Korea and Japan, *R. setigera* Michx. of North America, etc. The BB group includes nine Asiatic roses, but also the American *R. gymnocarpa* Nutt. CC is the *R. rugosa* group, including the American *R. nitida* Willd. DD is the group of *R. cinnamomea,* with several American species, such as *R. blanda, R. fendleri,* etc. EE, the group of *R. macrophylla* Lindl., is exclusively Asiatic, and almost confined to China. Hurst states that each of these groups may be considered a species, the various forms being ranked as subspecies under that carrying the oldest name. He does not, however, make the trinomials, and botanists are not likely to reduce in this manner a large number of roses hitherto regarded as of specific rank. In addition to the cited forms, it is explained that there are very numerous varieties. A subspecies is always homozygous for the subspecific characters, but a variety is frequently heterozygous for the varietal characters. Thus the subspecies ranks with the species rather than with the variety. It was found in the case of the AA roses, that so far as tested in crosses, they were fully fertile in the F_1 and F_2 generations,—an argument for considering them a single aggregate species. However, the most casual examination of the groups shows great diversity among the so-called subspecies. For example *R. nitida* is extremely unlike *R. rugosa,* and is usually placed in a different section. We are thus compelled to admit that the five groups are themselves complex, so that AA, BB, etc. are generalized conceptions, not implying genetic uniformity beyond a certain point. An alternate classification might conceivably include over fifty groups, instead of five. Nevertheless, there is a theoretical basis for the limited number of groups or aggregate species, namely that within these groups the sets of chromosomes are homologous in the sense that they are capable of pairing or forming synaptic mates, in consequence of which the hybrids should be fertile. Thus A may in fact be A_1, A_2, A_3, and so forth, through a series of modified forms, which are typically homozygous A_1, A_1, or A_2, A_2, etc., but can form hybrids A_1, A_2, etc. when artificially crossed, or where their ranges meet.

We now come to the polyploid roses, which are very numerous. First of all are the duplicational polyploids, such as AAAA, which does not differ from AA in the kind of chromosomes, but only in having two sets. They are thus like *Oenothera gigas,* and are found to exhibit a marked increase in size of all their parts. In certain cases triploids, as AAA, have been found among garden varieties. Hurst remarks that they may have arisen "from a duplicate gamete AA arising in a diploid AA, or from a cross between diploid AA and tetraploid AAAA, or from a bud sport derived from a somatic cell of a tetraploid AAAA that had lost a set of chromosomes."

The differential polyploids are those containing more than one kind of septet of chromosomes; these are divided into regular and irregular. Thus *Rosa huntii* Hurst (a new species from China) is AABB. *Rosa centifolia* L. is AACC. *Rosa palustris* Marsh is AADD. *Rosa davidi* Crep. from China is AAEE. *Rosa spinosissima* L. is BBCC. *Rosa pimpinellifolia* L. is BBDD. *Rosa multibracteata* Hemsl. & Wils. from China is BBEE. *Rosa virginiana* Mill. is CCDD, as also are *R. suffulta* Greene, *R. lunelli* Greene and others. No CCEE species is yet known. *R. pendulina* L. is DDEE. In addition to these tetraploids, there are hexaploids, as the beautiful *R. moyesii* Hemsl. & Wils. (AABBEE), which I saw growing at Cambridge; *R. wilsoni* Borr. (AABBCC) of Wales, Ireland and Scotland; the North American *R. nutkana* Presl. (AADDEE) and *R. engelmanni* Wats. (BBDDEE). There are even a few octoploid species, namely *R. tackholmii* Hurst n. sp. (AABBCCDD) from Iceland, and *R. acicularis* Lindl. (BBCCDDEE), circumpolar in subarctic regions.

The remaining group contains the irregular septet species, in which only part of the groups have synaptic mates. Such species are confined in nature to temperate Europe and Western Asia in an area approximately equivalent to that covered by the Pleistocene glaciation. Apparently they do not occur as far east as Lake Baikal; at least I believe none of the material I obtained there was so referable, though the results of Hurst's examination of it have not yet been reported. "All these species present the phenomenon at present unique in plants and animals, of a regular but unequal reduction division in female gametogenesis, which causes them to produce female gametes carrying from two to five times as many septets of chromosomes as their male gametes, so that their reciprocal hybrids are entirely different in their chromosome content and in their characters"—(Hurst, p. 891.) The pollen is only partly fertile, but the plants reproduce apomictically, and within their area flourish exceedingly. Here belong the familiar and variable dog-roses of England, Harrison and Blackburn[2] give a table showing the percent of fertile pollen in the *R. canina* group, ranging from those (*R. subcristata, R. fugax, R. coerulea*) in which the whole of the pollen aborts, to those (*R. senticosa, R. mollis*) in which it is 75 to 90 percent good. They tested many of these plants by castrating and bagging them, and without exception seeds were set. Comparison may be made with the condition in *Hieracium,* which is likewise polymorphic. The formulae have been worked out for a number of these irregular polyploids, and the following may serve as examples:

R. mollis Smith, CDDE, male gametes D, female CDE.

R. rubrifolia Vill. ADDE, male gametes D, female gametes ADE.

R. canina L. AABDE, male gametes A, female gametes ABDE.

R. rubiginosa L. ABBCD, male gametes B, female gametes ABCD.

Finally descriptions are given of numerous experiments in crossing the various roses, and it is stated that these appear to fully confirm, or to be fully in agreement with, the theory set forth. In a former paper Hurst[3] sets forth his ideas concerning the evolutionary significance of all these phenomena but since then he has somewhat modified his views. The following statement is quoted from a paper which he read before the Linnean Society in 1926, a typewritten copy of which he has kindly sent me: "The original decaploid species would most probably arise by duplication of an ancient diploid species under luxuriant conditions, just as duplicated forms have arisen under cultivation. This would be followed, in geological time, by differentiation of the five double septets of chromosomes and characters by duplicational segregations and gene mutations, thus giving rise within itself to the potentiality to throw off numerous new septet species by losses of septets. In this way evolution would be an alternating process, from diploid to

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[2] The Course of Pollen Formation in Certain Roses, with some deductions therefrom. Memoirs Horticultural Soc. New York, July, 1927.

[3] Chromosomes and Characters in Rosa and their significance in the origin of species. Genetics, XXXVIII (1925).

polyploid species (i.e., creative) and from polyploid to diploid species (i.e., emergent), according to geological conditions. This mechanism of alternating creative and emergent evolution in association with other secondary processes such as hybridization and chromosome mutations of the *Oenothera lata* type would also serve to explain the origin of the Tribes and Families of the Order Rosales, including the numerous extinct species eliminated by natural selection." (I independently reached similar conclusions, about the same time, as set forth in "Nature," April 10, 1926). It may be added that if polyploids are built up as postulated, they have two advantages as sources of divergent types. One is that if mutations occur once in so often, there is more chance for them in a polyploid with its greatly increased number of genes. The other is that such mutations, which might be injurious or fatal in a diploid may survive in a polyploid, until such time as circumstances favor some type of plant which they represent. On the question whether hybridization has played a large part in the evolution of roses, opinions differ, though no one disputes the fact that very numerous hybrids occur in nature. Blackburn and Harrison, in the paper already cited, conclude that the irregular polyploids arose through hybridization; and would also explain the regular or balanced polyploids in the same manner. In the latter case they suppose that the plants attained fertility "simultaneously with, and as a direct consequence of, a doubling in their chromosome complements". They dispute many of Hurst's findings in detail, and especially stress the case of *R. wilsoni,* which Hurst calls a true hexaploid species, but which they assert to be a hybrid between *R. pimpinellifolia* and *R. tomentosa,* the latter the pollen parent. Such a hybrid, if I understand Hurst's notation, should apparently come to nothing, but Blackburn and Harrison state that theoretically it ought to have 14+7 as its somatic number of chromosomes, whereas it actually has 42. (This number 42 agrees with the view that it is a hexaploid species). They add: "Obviously chromosome doubling by some means or other has occurred, but, what is most noteworthy, although the reciprocal hybrid is unbalanced and sterile, this is balanced and fertile. Thus we have generated before us, by the union of an egg with 14 chromosomes and a pollen grain with 7, a fully fertile hexaploid rose." In other words, a veritable species has been produced by hybridization.

The subject is so complex and the investigations are so new, that it is unreasonable to expect any approach to finality. Yet it is evident that, no matter what may be said about this or that alleged fact, there is here opened up a most fertile field for research, with reasonable expectations of seeing into the processes of evolution in a manner never before considered possible. Taxonomy, also, takes a new meaning, and may attain more precision than seemed possible in such polymorphic genera. We are encouraged to examine the face of nature, searching for evidence in all directions. New types may come into existance to perish at once, or may survive a little while, and eventually perish, or may spread in ever widening circles. Thus local forms are not necessarily relict species, survivors of a once mighty host. Furthermore, as far as can be seen, there is no reason a species should not be polyphyletic, in the sense of arising more than once from similar ancestors, in different places. When this occurs, there will be a probability that the ancestors will not be exactly alike, but will differ in at least some genes, so that the separate colonies (as we call them) of a species may be distinguishable on very close inspection. That this is true of varieties, we are all aware, and no one doubts that the identical gene mutations occur many times independently.

It will be interesting to see if novel climatic conditions have any effect on the variable roses. There is a member of the *R. canina* group supposedly naturalized in Mexico. At Wallangara, on the southern border of Queensland, I found plenty of the irregular pentaploid *R. rubiginosa* growing. These exotic colonies should be closely watched. If their chance for differentiation depends on hybridization, then they are likely to be more constant than at home. Also at Wallangara, *Raimannia odorata*, another plant of interest to the geneticists, has run wild.

It is possible to postulate a scheme of evolution for *Rosa* which requires neither the breaking up of a hypothetical decaploid nor the building up of polyploids by hybridization. Hurst's diploid aggregate "species" may have developed from an ancestral diploid by a process of gene mutations, exactly as the segregated species or subspecies have developed within these aggregates. Then the polyploids may owe their origin to chromosome duplication, and the diversification of their septets (groups of seven chromosomes) to subsequent gene mutation. This implies parallel mutation, which is known to occur. Vavilov has shown in the most striking manner how parallel variations, through long series, arise in related genera of plants, where no question of hybridization is involved. On this basis a tetraploid AABB rose may have evolved from a diploid AA, and the B septets it contains may only simulate those of the diploid BB, without having any genetic connection. This leaves the irregular septet forms as probably of hybrid origin, and as Hurst remarks, several of them are actually known to be hybrids. With regard to the fossil roses, it must be remembered that the Florissant species date from the Miocene, and occur with a flora which is not more primitive than that of the present day. Chaney[4] has identified one of the Florissant species (*Rosa hilliae* Lesqx.) in the Bridge Creek (Tertiary) beds of Oregon, his material consisting of detached leaflets and a piece of stem with prickles. There is no more basis for referring this material to *R. hilliae* than to any one of several living species; nor, I think, any reasonable probability that it belongs to Lesquereux's species. Chaney speculates on the possibility that all the Florissant rose leaves belong to one species, and suggests that *R. ruskiniana* Ckll. represents the fruit of this species. As a matter of fact, *R. ruskiniana* was based on a bud and its fruit is unknown. I think there is no doubt that *R. hilliae* and *R. wilmattae* Ckll. are quite distinct, but *R. scudderi* Knowlton may be a variation of *R. wilmattae* and the other two, based on a bud and immature fruit respectively, probably belong with some of the leaves.

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[4] Geology and Paleontology of the Crooked River Basin with special reference to the Bridge Creek Flora. Publ. 346, Carnegie Inst. of Washington (1927), p. 123.